

ADAPTATION OF TEST SHAPE FOR BURROWING AND LOCOMOTION IN SPATANGOID ECHINOIDS

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ABSTRACT. In considering ventral shape and longitudinal sectional outline of the test in fourteen living spatangoid species, four types can be recognized: flat, globular, wedge-shaped, and domed, with two intermediate series. Although the basic arrangement of spines is common to all, differences in test profile impart different attitudes to the spines and hence affect their function for burrowing. Three different burrowing mechanisms are recognized, which are the consequence of specific test profiles. Each burrowing mechanism corresponds to a specific burrowing depth and to sediment grain size. The globular urchins burrow by excavating frontal sediment and accumulating it on their backs. This is the consequence of the elevated plastron and the stern-like postero-ventral shape, and is effective for the urchins living deep in sand. Flat urchins live close to the sediment surface and burrow by pushing excavated sediment to the posterior sides of the test. The wedge-shaped type moves through the sediment by thrusting into the sediment in front rather than excavating it, rocking its anterior end up and down. This is effective in soft, cohesive mud; the wedge shape is essential for the repeated rocking motion. The overall test profile of each type also accords with a distinctive habitat. The flat profile of shallow-burrowing sand-dwellers keeps them stable against current scouring. The globular profile of deep-burrowing sand-dwellers helps support the burrow wall. The test shape is seemingly less constrained than the arrangement of spines, and a wide variety of test shapes enables spatangoids to live in various environments.

THE order Spatangoida is a group of irregular echinoids adapted to an infaunal mode of life. They appeared in the Early Cretaceous, and diversified during the Late Cretaceous and Tertiary (Fischer 1966). Today, spatangoids live in littoral to bathyal zones burrowing to various depths in various types of sediments. Burrowing is the principal means by which spatangoids collect microphagous food effectively from the sediment.

Spatangoids have a wide variety of test shapes. Some are globular or hemispherical; others flat or wedge-shaped. Each type of test morphology is apparently related to a specific habitat, as discussed later. This is in marked contrast to many other irregular echinoids whose test profiles are more or less the same within respective groups, each group living in a particular environment. The test profile of spatangoids, therefore, presumably has a greater functional significance to enable them to live in a variety of environments.

However, little attention has been paid to the functional design of the test profile in spatangoids, despite many detailed descriptions of test shape for classification or discussion of evolutionary lineages (e.g. Rowe 1899; Mortensen 1951; Kermack 1954, Ernst 1972; Stokes 1977). Nichols (1959a, 1959b) noted that differences in test profile are related to burrowing depth, based on the observations of some living spatangoids. McNamara and Philip (1980) showed that the test profile in schizasterid lineages changes from globular to wedge-shaped as the grain size of sediment decreases. These changes of test profiles are generally thought to make burrowing easier (e.g. Smith 1984), although the way in which the test profile works for burrowing has not been fully discussed. McKinny (1988) attempted to explain the effectiveness of wedge-shaped profiles from the viewpoint of burrowing mechanism. This was, however, deduced without actual observation of burrowing behaviour.

The burrowing mechanisms of several spatangoids, including *Echinocardium cordatum*, *Spatangus purpureus* and *Meoma ventricosa*, have been studied in aquaria and in their natural environments (e.g. Nichols 1959a; Kier and Grant 1965; Chesher 1968, 1969). Based on these observations, only

a single type of burrowing mechanism has been recognized so far. The spatangoids have a complex arrangement of functionally and morphologically distinct spines on the test surface (Nichols 1959a; Smith 1980). Spines are arranged in the same basic way in all spatangoids (Smith 1980; Smith and Crimes 1983). Because of this common spine arrangement, previous workers have assumed that all spatangoids burrow in the same way.

Spatangoids, however, show a wide variety of test shapes. It is natural to assume that the different test shapes give spines different attitudes and directions of movement, relative to the surrounding sediment. Accordingly, the function of spines and the burrowing mechanism may also differ. This is the basic idea with which the functional significance of test profile in the spatangoids in relation to their burrowing mechanisms must be approached (Kanazawa 1991). Observations were made on the movement of spines during burrowing behaviour of spatangoids with different test shapes living in distinctive habitats. I recognize three different burrowing mechanisms that are reasonably explained by differences in test shape and resultant function of spines. Each burrowing mechanism corresponds to a specific habitat.

The design of the test profile is, of course, not fully explainable simply in terms of its function for burrowing. Some test shapes apparently deviate from the paradigm for burrowing. These shapes have other functions, probably related to the characteristics of the habitat, as discussed later.

Fourteen living spatangoid species distributed among thirteen genera and belonging to six families are examined in this study (Table 1). The specimens were obtained from around the coast of Japan by dredging with a beam trawl, Smith-McIntyre grab, box corer, and directly by scuba diving.

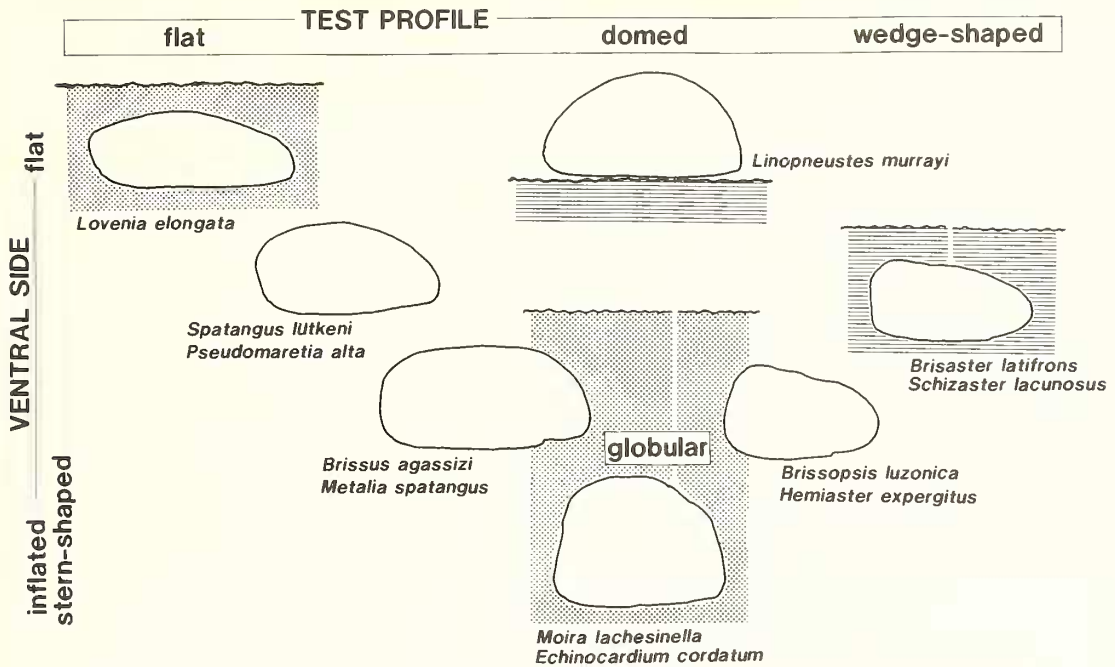
TABLE 1. Habitats of the spatangoids examined in the study.

Species	Locality	Depth (m)	Substratum	Observation of burrowing behaviour in aquarium
<i>Brisaster latifrons</i> (Agassiz, 1898)	Suruga Bay	300–1200	Mud	°
<i>Brissopsis luzonica</i> (Gray, 1851)	Suruga Bay	280–1700	Muddy sand	°
<i>Brissus agassizii</i> Döderlein, 1885	Toyama Bay	1–3	†	°
<i>Echinocardium cordatum</i> (Pennant, 1777)	Tsuruga Bay	10	*	°
<i>Gymnopatagus magnus</i> Agassiz and Clark, 1907	Off Ohtsuchi	1300	Muddy sand	
<i>Hemiaster expurgitus</i> Lovén, 1874	Suruga Bay	430–1100	Mud	
<i>Linopneustes murrayi</i> Agassiz, 1879	Off Kushimoto	900–1200	Mud	
<i>Lovenia elongata</i> (Gray, 1845)	Tsuruga Bay	1–3	*	°
<i>Metalia spatangus</i> (Linnaeus, 1758)	Iriomote Island	1–3?	†	
<i>M. sternalis</i> (Lamarck, 1816)	Ise Bay	90–120	?	
<i>Moira lachesinella</i> Mortensen, 1930	Tsuruga Bay	1–3	*	°
<i>Pseudomaretia alta</i> (Agassiz, 1863)	Tsuruga Bay	20	Sand	
<i>Schizaster lacunosus</i> (Linnaeus, 1758)	Maizuru Bay	10–30	Mud	
<i>Spatangus luetkeni</i> Agassiz, 1872	Kashima Sea	90–300	Sand	

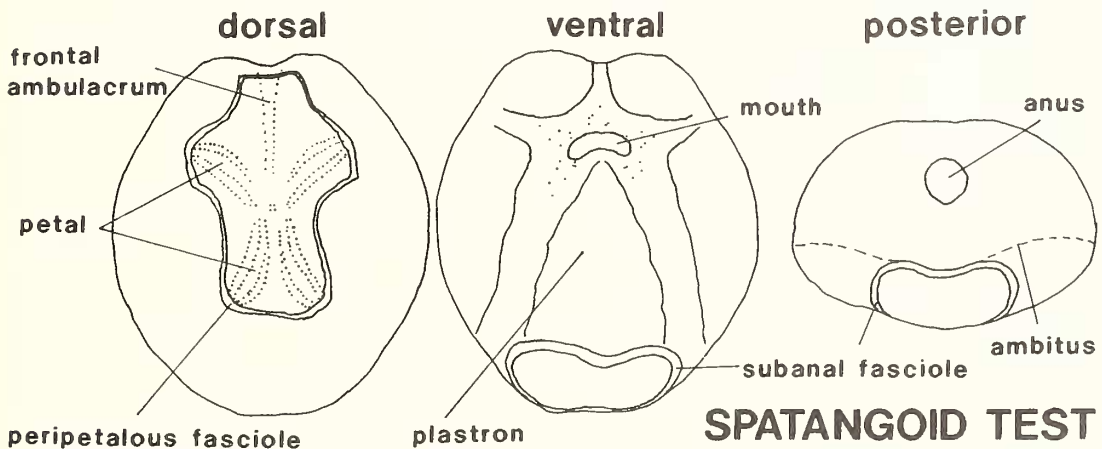
* Silty fine to medium grained sand; † gravelly coarse-grained sand; ° observed behaviour.

TEST PROFILE AND HABITAT OF THE SPATANGOIDS

Based on test profile (shape of ventral side and outline of longitudinal section), the spatangoids examined can be grouped into four types with two series of intermediate forms between them (Text-fig. 1). The four types represent extreme morphologies among various test shapes and are termed here: flat, globular, wedge-shaped and domed types, after their profiles. The morphological

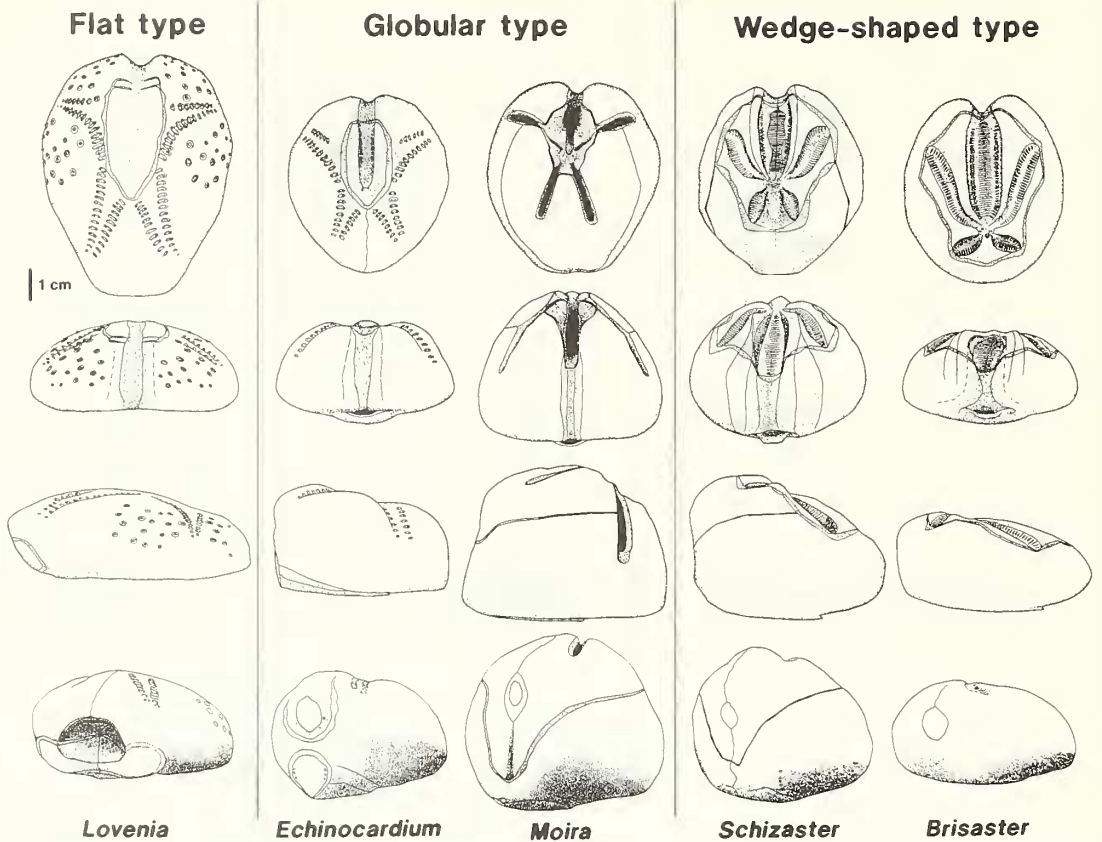


TEXT-FIG. 1. Spectrum of test shapes and habitats seen in the spatangoids. Each type of the test shape apparently corresponds to a specific habitat: urchins having flat profiles with flat ventral sides live at shallow depth in sand; those having globular profiles with inflated ventrals live deep in sand; wedge-shaped urchins live in mud. Urchins having a domed profile with a flat venter are epifaunal living on mud. The habitats of other urchins having intermediate profiles are shown in Text-figure 4.



TEXT-FIG. 2. Main features of the test of a spatangoid *Brissopsis luzonica*. Ambitus is the greatest horizontal circumference of the test.

characteristics of each type are noted below with their observed habitats. Terminology of the morphology used in this study is given in Text-figure 2.



TEXT-FIG. 3. Test morphology of the three types showing morphological extremes in test profile. Dorsal, anterior, lateral and latero-posterior views are shown from top to bottom for representative genera.

Globular type

Echinocardium cordatum and *Moira lachesinella* belong to this type (Text-fig. 3). The test is highly inflated, and box-shaped or globular in extreme cases. The ventral side is weakly inflated and the central plastron area is elevated forming a keel-like ridge. The ambitus migrates markedly upward in the middle and the posterior parts, and inclines towards the anterior. The postero-ventral region has a stern-like shape, being curved slightly inward from the lateral ambitus to the plastron. The test is small, less than 50 mm in longitudinal diameter in the adult.

E. cordatum and *M. lachesinella* were observed at 1–3 m water depth in Tsuruga Bay, on the Japan Sea coast. They burrow in poorly sorted, silty fine to medium grained sand with the apex 100–200 mm below the sediment surface. *E. cordatum* was also obtained from silty fine grained sand at a depth of 10–30 m in Ise Bay on the Pacific coast, and from silt in Maizuru Bay on the Japan Sea coast. *E. cordatum* from both localities burrowed to 50–100 mm in aquaria with their native muddy sediments. These observations are consistent with many other reports on the habitat of *E. cordatum*, such as that of Nichols (1959a) from the British Isles and Higgins (1974) from the British Isles and New Zealand.

Flat type

Lovenia elongata belongs to this type (Text-fig. 3). The test profile is elongated and low with a flat

ventral surface. The broadest part of the test is located slightly anteriorly. The test is large, exceeding 80 mm in longitudinal diameter in adults.

At Tsuruga Bay, *L. elongata* is usually found together with *E. cordatum* and *M. lachesinella*. It burrows much shallower than these species, with its apex 10–20 mm below the sediment surface, as reported by Ferber and Lawrence (1976) from the Gulf of Aqaba.

Wedge-shaped type

Brisaster latifrons and *Schizaster lacunosus* belong to this type (Text-fig. 3). The test profile is wedge-shaped with the dorsal side sloping anteriorly. The broadest part of the test is located in the posterior, and the test tapers toward the anterior. The ventral surface is weakly inflated, but the plastron area is almost flat. The test is relatively small, about 40–70 mm in longitudinal diameter in adults.

B. latifrons lives in soft muddy bottoms at 300–1200 m depth in Suruga Bay on the Pacific coast of central Japan. Some urchins were obtained *in situ* by box corer. They were observed to burrow with the apex 20–50 mm below the sediment surface. Also, *S. lacunosus* taken from mud at 10–30 m depth in Maizuru Bay probably lives by burrowing 20–50 mm deep in the substrate, as estimated from aquarium observation with the original sediment of the sampling locality.

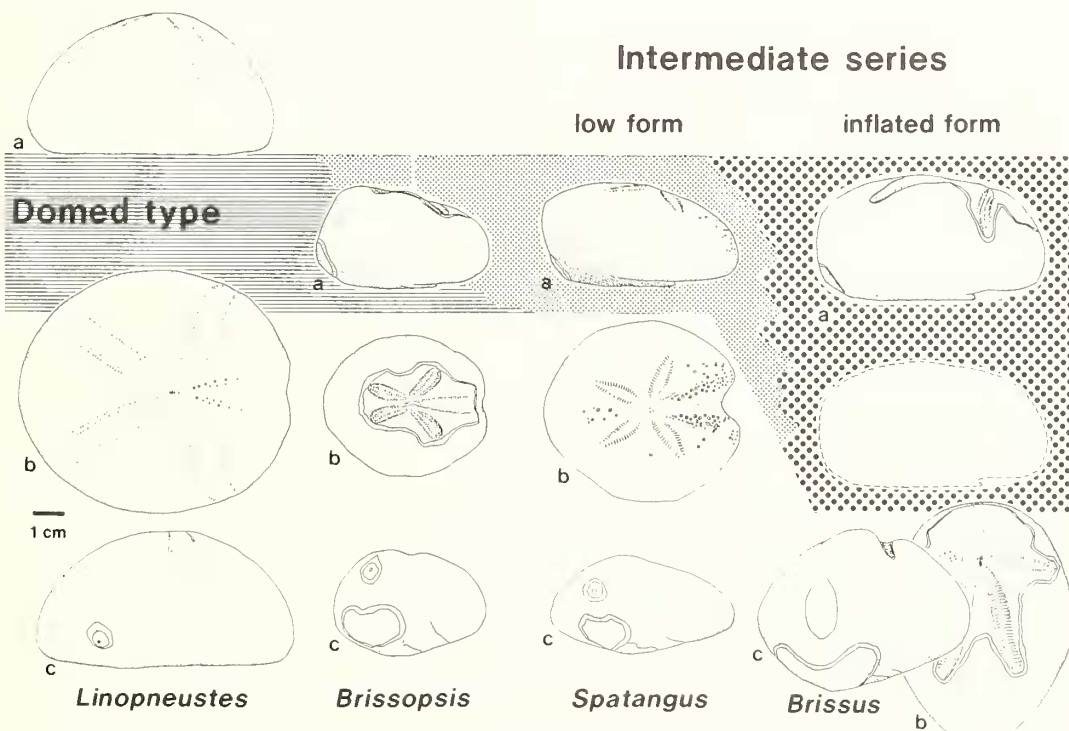
Domed type

Linopneustes murrayi belongs to this type. The test is dome-shaped or hemispherical with a highly inflated dorsal side and a flat ventral side (Text-fig. 4). *L. murrayi* is found on muddy bottoms of the bathyal and abyssal zones where it lives epifaunally. In Suruga Bay, this urchin has been photographed, moving around on the sea floor and leaving a trail behind it (Okada *et al.* 1980; Ohta 1983).

Intermediate series

low form

inflated form



TEXT-FIG. 4. Test shapes and habitats seen in the spatangoids of the domed type (extreme left), and three intermediate forms (others). a, side views and habitats; b, dorsal views; c, latero-posterior views.

Intermediates between globular and flat types

Two forms of test profile (inflated and low profile) are recognized in this series (Text-fig. 1). *Brissus agassizii* and *Metalia spatangus* belong to the former, *Spatangus luetkeni* and *Pseudomaretia alta* to the latter. The ventral side of the inflated form is weakly inflated, and the plastron area is elevated, whereas the ventral side of the flat form is flat except for the elevated plastron area. The postero-ventral part of both forms is stern-like, similar to that of the globular type (Text-fig. 4).

The inflated form *B. agassizii* was found in gravelly, coarse grained sand near the tidal zone in Toyama Bay, usually burrowing 30–50 mm deep, sometimes to about 200 mm below the surface.

The low form *S. luetkeni* was obtained from sandy bottoms of the Kashima Sea at 90–300 m depth and of the Kumano Sea at 90–110 m depth, both on the Pacific coast. *P. alta* lives in sandy bottoms at about 20 m depth in Tsuruga Bay. It presumably burrows less than 100 mm deep, because urchins of this species can be obtained with the dredge, which samples sediment down to this depth. These weakly inflated urchins live in calmer and deeper environments than the flat type *Lovenia elongata*.

Intermediates between the globular and wedge-shaped types

Brissopsis luzonica and *Hemiaspergites* are intermediate between the globular and wedge-shaped types (Text-fig. 1). Their tests are inflated but their dorsal side gently slopes anteriorly. The ventral side of the test is weakly inflated, and the plastron area is elevated, forming a stern-like shape (Text-fig. 4). Urchins of this form are usually obtained from muddy sand bottoms in the bathyal zone and sometimes from muddy bottoms in association with the wedge-shaped type *Brisaster latifrons*. *Brissopsis luzonica* was obtained *in situ* from Suruga Bay by box corer, burrowing to a depth of 30–50 mm.

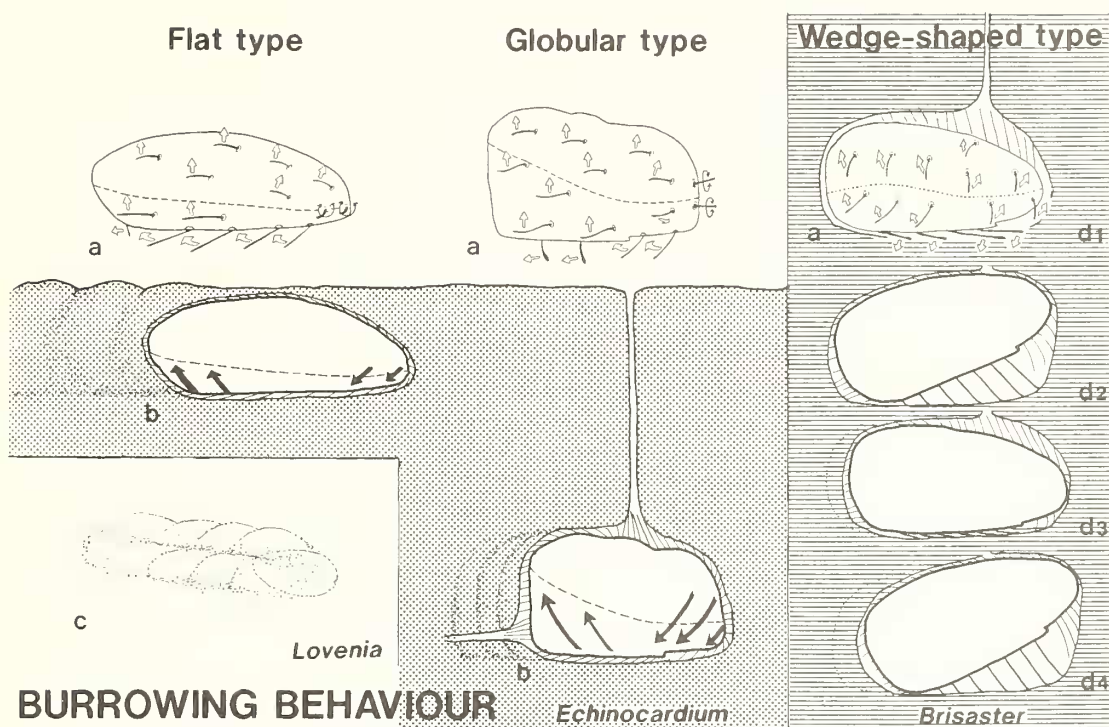
FUNCTION OF SPINES AND THE BURROWING MECHANISM IN SPATANGOIDS

Spatangoids have a complex arrangement of spines differentiated into functionally and morphologically distinct areas on the test surface (Nichols 1959a; Smith 1980). There are six important groups of spines: plastron, latero-ventral, anterior, dorsal, sub-anal tuft, and apical tuft. Arrangements of these spines are basically the same among all spatangoids (Smith 1980; Smith and Crimes 1983). The function of these spines for moving and burrowing has been precisely studied for *Echinocardium cordatum* (e.g. Nichols 1959b; Smith 1980). Previous workers seem to have a common understanding that respective groups of spines have the same function in all spatangoids, because of their common arrangement. In this paper, the apical tuft and the subanal tuft spines are disregarded, because in all the spatangoids examined their functions are confined to the construction and maintenance of the respiratory funnel and posterior tunnels, as observed by Nichols (1959a), Chesher (1963) and Buchanan (1966).

Whereas previous observations of the burrowing activity were made mainly of urchins digging into sediment from the surface, I have observed them in living position within their burrows. The infaunal spatangoids usually burrow horizontally and take food from the sediment, so that burrowing through the sediment is normal, or 'daily', activity. The activity in the sediment was observed when the urchin appeared at the bottom of, or at the side wall of, an aquarium. Burrowing behaviour was recorded using a video camera for analysis.

The movement of spines was also interpreted from the morphology of tubercles. Smith (1980) showed that the direction of the power stroke of spines can be inferred from the development and direction of the areole enlargement; the stroke is produced by a muscle whose size and direction can be deduced from the morphology of its scar (areole) at the marginal area of the tubercle.

The spatangoids used for both behavioural and morphological observations were: *Echinocardium cordatum* and *Moira lachesinella* for the globular type, *Lovenia elongata* for the flat type, *Brisaster latifrons* and *Schizaster lacunosus* for the wedge-shaped type, and *Brissus agassizii* and *Brissopsis luzonica* for the intermediates.



TEXT-FIG. 5. Three different types of burrowing mechanism in spatangoids. *a*, postures of spines and the direction of the power strokes (open arrows); *b*, movement of excavated sediment (solid arrows); *c*, a set of two mounds formed on the sediment surface behind the flat type *Lovenia elongata*; *d*, two cycles of rocking motion in the wedge-shaped type.

TYPES OF BURROWING MECHANISMS IN RELATION TO TEST SHAPE

Three different burrowing mechanisms were recognized through aquarium observations, and were employed by the three morphological types: globular, flat and wedge-shaped, respectively. The different burrowing mechanisms are derived from differences in test shapes and the resultant difference in functions of spines. Also, each burrowing mechanism corresponds to a specific habitat, as discussed below. Text-figure 5 shows the direction of spines on the test surface, the direction of power strokes of spines, and the burrowing mechanism of the three types.

Globular type

Burrowing behaviour. Globular *Echinocardium cordatum* and *Moiria lachesinella* burrow in fine to medium grained sand with the apex 100–200 mm below the surface of the sediment in the aquarium. They move forward at about 50 mm per hour. The rowing action of the plastron spines provides the principal horizontal thrust for forward locomotion (Text-figs 6–7), while the anterior spines excavate the frontal wall of the burrow with their rotary action (Text-fig. 6). The excavated sediment is transported by the metachronal wave action of the latero-ventral spines to the latero-posterior region of the test (Text-figs 6, 8A–B), and then moved upward toward the ambitus along the test surface (Text-fig. 8C). Consequently, transported sediment is accumulated on the back of the animal. While the ventral spines are working, the metachronal waves formed by the dorsal spines are migrating from anterior to posterior. The movement of the dorsal spines probably supports and maintains the ceiling of the burrow, transporting a protective mucus coat secreted from the fasciole

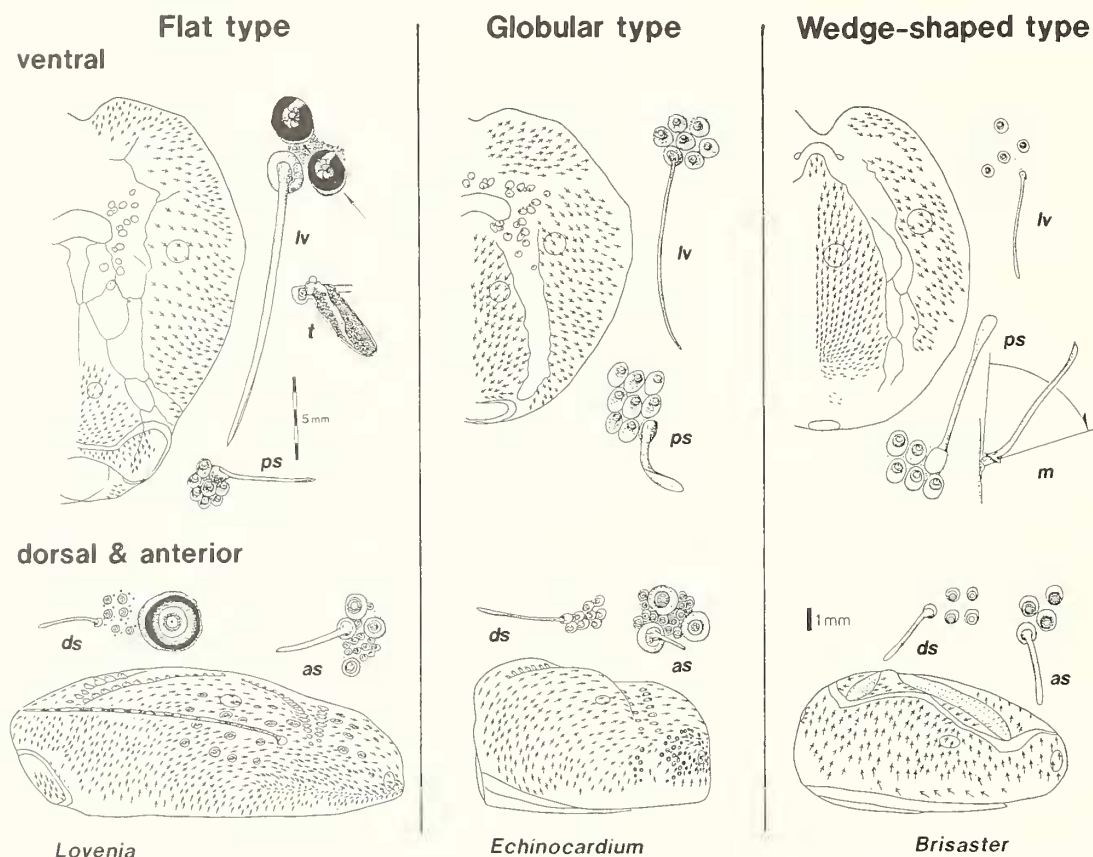
to cover the whole dorsal surface, as described for *E. cordatum* by Pequignat (1970) and Smith (1980).

The urchin usually burrows deeply under the sediment surface, where the pressure from surrounding sediment is relatively high by virtue of its weight. Under such conditions, the test shape is advantageous in that it produces the space for transporting and accumulating excavated sediment.

Function of spines related to test shape. The burrowing mechanism of the globular type is closely related to the elevated plastron and the stern-like shape of the postero-ventral of the test.

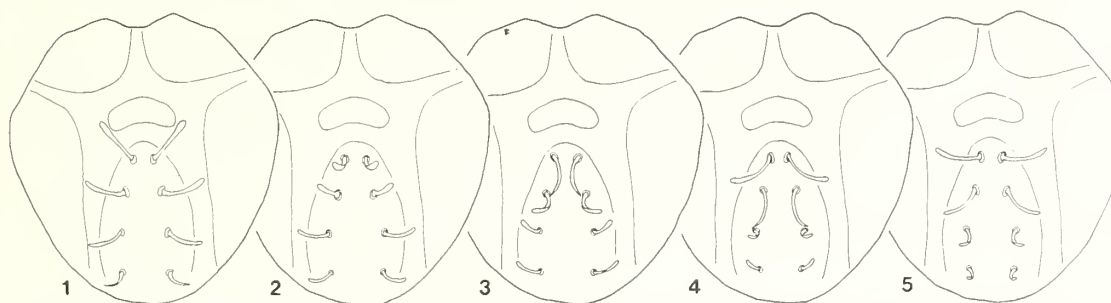
1. *Plastron spines.* The elevated plastron brings the plastron spines into contact with the floor of the burrow (Text-Fig. 5), so that the plastron spines support the test, and their backward-directed power strokes provide the principal thrust for forward locomotion. The anteriorly curved and strongly spatulate plastron spines makes the spatulate face contact with the bottom sediment of burrow and provide the strong thrust (Text-fig. 6).

2. *Latero-ventral spines.* The elevated plastron also provides space between the latero-ventral



TEXT-FIG. 6. Morphology of spines and tubercle arrangement in the three morphological types. lv, latero-ventral spines; t, longitudinal section through a latero-ventral tubercle with deeply sunken areole; ps, plastron spines; m, movement of a plastron spine of the wedge-shaped type seen from side view; ds, dorsal spines; as, anterior spines. Arrows on test surface indicate the direction of areole enlargement, i.e. the direction of maximum power stroke. The extremely long dorsal spines of *Lovenia elongata* are used for righting and defence.

Plastron spines



TEXT-FIG. 7. A cycle of rowing action of the plastron spines in *E. cordatum*, drawn from video pictures. Movements of some spines are shown from left to right. Spines swing almost perpendicular to the test surface during the power stroke, and pass closer to it during recovery. The movements of adjacent spines are synchronized, and the 'wave' of strokes passes from anterior to posterior.

region of the test and the floor of the burrow, enabling the latero-ventral spines to transport excavated sediment to the posterior. The latero-ventral spines are moderately long, gently curved latero-posteriorly and have adambital-facing spatulate tips (Text-fig. 6). The spoon-like shape of the latero-ventral spines facilitates sediment transport.

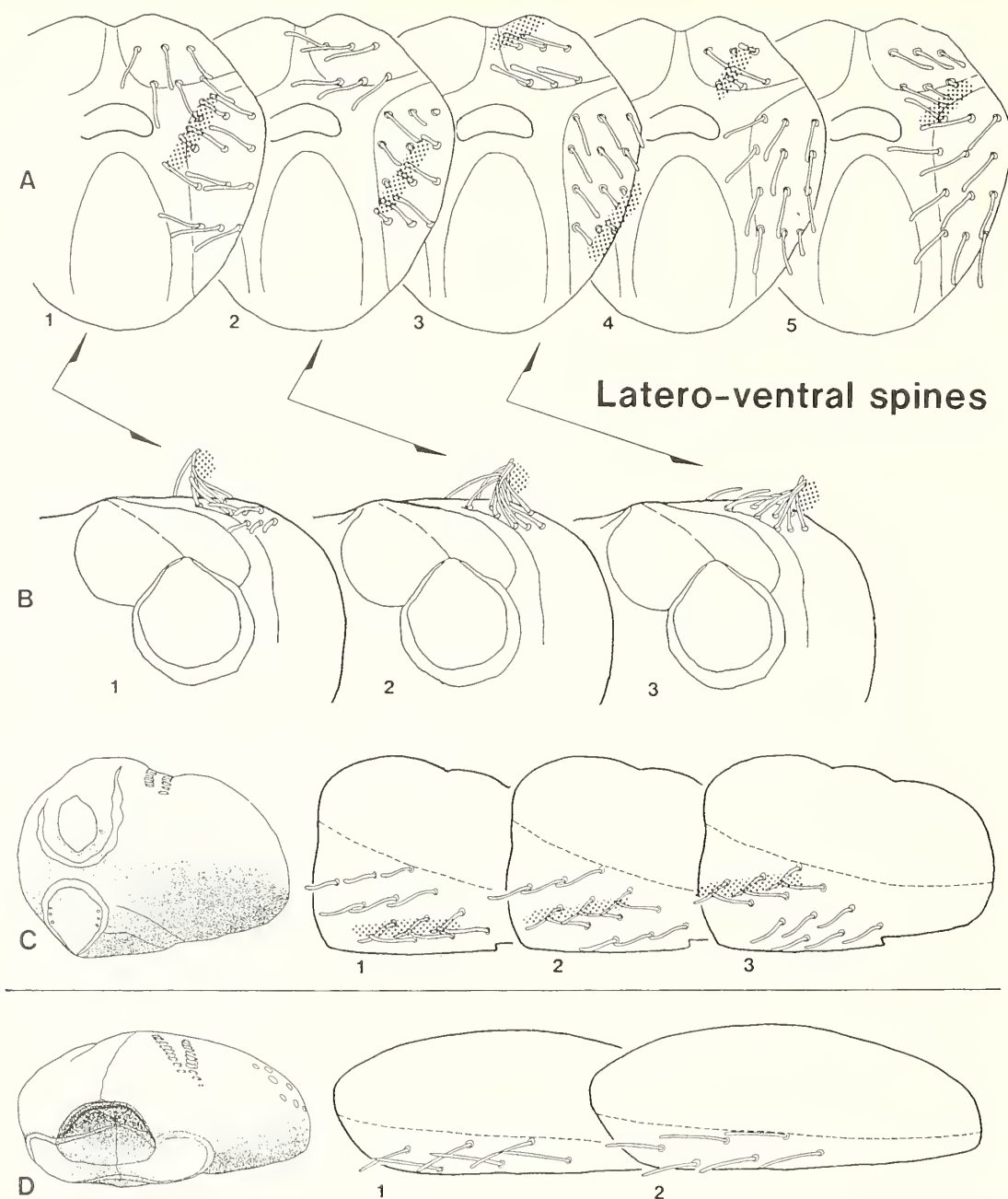
The stern-like shape of the postero-ventral region directs the power stroke of the latero-ventral spines upward rather than backward (Text-fig. 8C). Accordingly, the sediment transported to the latero-posterior region is moved upward toward the ambitus along the test surface, and is then accumulated on the back of the animal. The stern-like shape also produces an empty space behind the animal as the urchin moves forward. The stern shape of the postero-ventral part therefore enables the urchin to accumulate the rejected sediment on its back.

3. *Dorsal spines.* The dorsal spines are $7-8 \text{ mm}^{-2}$ in number in *E. cordatum* and *M. lachesinella*, inclined posteriorly, with the spatulate tips facing the burrow wall (Text-fig. 6). The dense dorsal spines provide a canopy which supports and maintains the ceiling and walls of the burrow. The dorsal side always bears the load of the overlying sediment, so that this function is probably important. The backward inclination of the dorsal spines is significant to support the burrow without interfering with forward locomotion.

4. *Anterior spines.* *E. cordatum* has specific excavatory spines scattered on the anterior face of the test (Text-figs 5-6). They loosen and excavate the frontal wall of the burrow, a function which has been repeatedly described by Nichols (1959a), Smith (1980) and others.

Flat type

Burrowing behaviour. The flat type, *Lovenia elongata*, burrows in fine to medium grained sand with its apex 10-20 mm below the surface. The urchin is usually stationary in its burrow, and moves forward sporadically at intervals of 3 to 30 minutes. It moves about 200 mm a day in the aquarium. In this flat type urchin, the latero-ventral spines provide the principal thrust, unlike those of other types. Just after the urchin stops moving forward, the anterior spines around the anterior ambitus loosen the frontal wall of the burrow. The frontal sediment collapses onto the anterior floor of the burrow, and the latero-ventral spines transport the sediment to the latero-posterior end of the test with a metachronal wave action. Then the spines push the transported sand above both posterior sides of the test and into the surrounding sediment. A double mound of sediment was observed on the sediment surface behind a burrowing urchin in an aquarium (Text-fig. 5). While the ventral



TEXT-FIG. 8. Action of latero-ventral spines in *E. cordatum* (A–C) and *L. elongata* (D). A, ventral view; B, inverted view seen from the postero-ventral side; C–D, latero-posterior view to the left, and side view to the right. Movements of latero-ventral spines are shown from left to right. The rotation of each of the spines defines a flattened ellipse, swinging posteriorly away from the ventral surface during the power stroke and returning closer to it through the inside pass during the recovery stroke. The movements of nearby spines are synchronized, and the wave of motion passes from the anterior end to the latero-posterior end. The anterior-most and posterior-most spines are at about the same stage of the cycle, and the waves of opposite sides of the test move alternately.

spines are working, the dorsal spines are also motionless; they probably support the sediment overlying the urchin.

The burrowing mechanism adopted by the flat type is only effective for the urchin burrowing close to the sediment surface where excavated sediment can be easily pushed out into the surrounding sediment.

Function of spines related to test shape. The mechanism of burrowing employed by the flat type urchin arises from the flat ventral side of the test, although the flat ventral side itself may not be a design for burrowing, as discussed later.

1. *Plastron spines.* In *L. elongata*, most of the plastronal area is naked, and small, slender and less spatulated plastron spines occur only in a small area immediately anterior to the subanal fasciole (Text-fig. 6). The plastron spines of the flat type urchin do not provide effective thrust, because they are too small and few in number. The function of the plastron spines in this type is subordinate.

2. *Latero-ventral spines.* The flat venter brings the latero-ventral spines into contact with the bottom of the burrow. These spines, which are much larger than the plastron spines, support the test and their backward power strokes push the animal forward, as described by Ferber (1976). The areoles of the latero-ventral tubercles in *L. elongata* are deeply sunken and form large bulges on the inside of the test named camellae (Text-fig. 6). The latero-posterior side of the areole is much more sunken than the opposite side. The areoles provide the attachment area for the extremely long and thick muscles which produce the powerful back and outward spine strokes. The stout and large latero-ventral spines driven by strong muscles enable the animal to provide principal thrust as well as to push out the excavated sediment.

Latero-ventral spines also play a principal role in fast diving into sediment. The latero-ventral spines of the flat type urchin excavate the sediment under the animal rapidly and push it out on both sides of the test (Text-fig. 9). It takes about 40–140 seconds for the animal to disappear under the sand, which is about one-tenth of the time taken by globular types: 8 minutes for *E. cordatum* and 10 minutes for *M. lachesinella*.

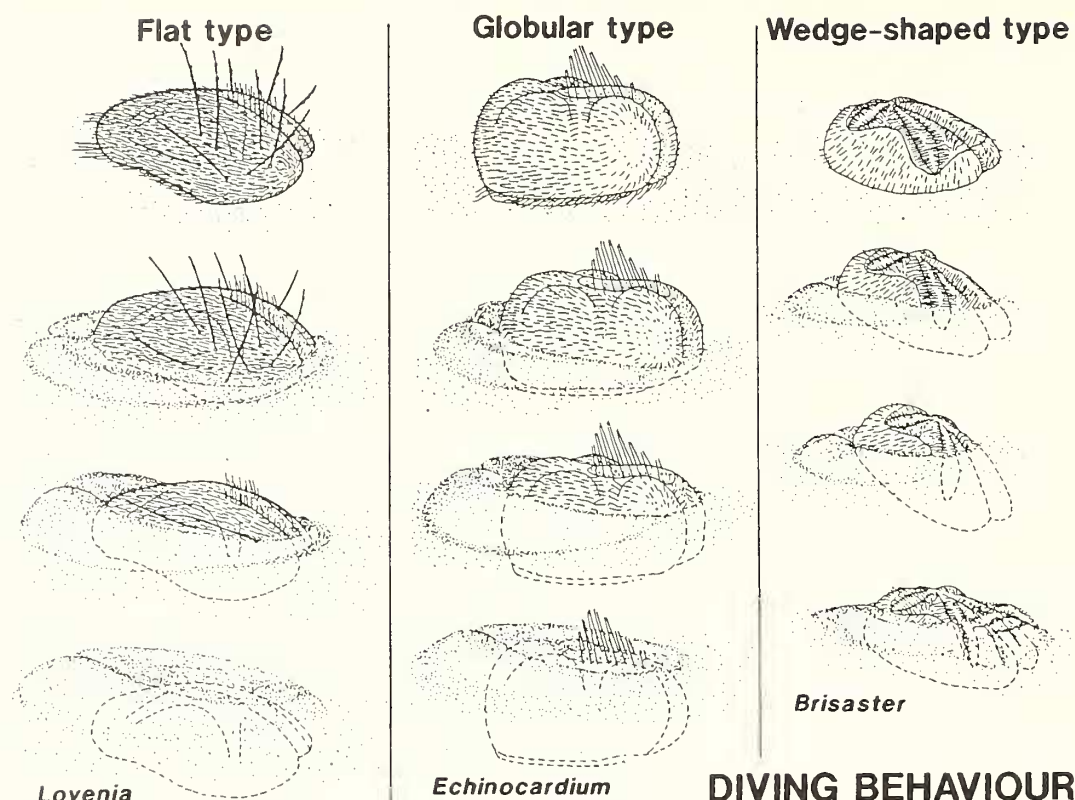
3. *Dorsal spines.* The dorsal spines of *L. elongata* are sparse and almost motionless, compared with those of the globular type urchins. The spines are, however, probably used to support the ceiling of the burrow and to maintain space for water circulation.

The flat type urchin has extremely long, stout, posteriorly pointing spines on the dorsal side amongst the uniform covering of small dorsal spines (Text-fig. 6). These long spines play no significant role in burrowing and locomotion. They are, however, used for defence and righting, when the urchin is exposed on the sediment surface and turned upside down.

4. *Anterior spines.* Specific excavatory spines, which are slightly larger than surrounding spines, are scattered around the anterior ambitus (Text-fig. 6). They loosen the frontal wall of the burrow with slow, weak rotary action.

Wedge-shaped type

Burrowing behaviour. *Brisaster latifrons* and *Schizaster lacunosus* burrow in soft mud with their apices 20–50 mm below the surface, and move forward at a few centimetres per hour in the aquarium. The plastron spines provide the thrust for forward locomotion; however, the motion of the test is different from the horizontal movement of the globular type. The wedge-shaped type urchins move obliquely upward and thrust into the frontal wall of the burrow (Text-fig. 5). Consequently, the anterior end of the test is raised and the body axis becomes oblique, at about 30° to the horizontal (Text-fig. 5). This motion produces cracks on the sediment surface when the urchin burrows to a depth of 20 mm below the surface. While the urchin maintains its oblique posture, the latero-ventral spines at the anterior end of the test scrape the lower part of the frontal wall of the burrow. Only a small amount of sediment is scraped; several mud pellets, about 0.5–1 mm in diameter bound with mucus, are transported towards the posterior end of the test. The movement



TEXT-FIG 9. Diving behaviour of the spatangoids. Successive stages are shown from top to bottom. Note that wedge-shaped urchins dive by a repeated rocking motion, different from other types. As the wedge-shaped *Brisaster latifrons* scrapes the sediment beneath the animal with the latero-ventral spines, the test sinks into the sediment, declining towards the anterior. When the body axis declines at about 30° to the sediment surface, the urchin pushes into the sediment with the thrust of the plastron spines; at the same time the anterior end rises slightly and conversely the posterior end sinks, and the body axis returns to the horizontal. The urchin repeats the rocking motion four times for complete burial, with a forward displacement of about 40 mm. The whole process takes about an hour.

of the latero-ventral spines is very slow and their metachronal action is indistinct. It takes about half a minute to transport a mud pellet from the anterior to the posterior end.

On the dorsal side of the test, while the urchin maintains its oblique posture, weak but continuous waves formed by the dorsal spines pass from anterior to posterior. Each wave migrates very slowly, at a speed of about 2 mm per second, which is about one-eighth that of the globular type *M. lachesinella*. The wave action of the dorsal spines probably transports the protective mucus coat secreted by the fasciole. After the urchin has maintained the oblique posture for about 3–5 minutes, the dorsal spines are pulled strongly upwards, and the tips of the spines push against the ceiling of the burrow. Accordingly, the test is moved downward to the bottom of the burrow and returns to the horizontal (Text-fig. 5).

These successive movements of the animal produce a slight forward displacement (about 3 mm for an animal 32 mm long). It takes about 3–5 minutes for each cycle of forward locomotion. The wedge-shaped urchins push directly into the frontal sediment rather than excavating it, and move through the sediment by means of a repeated rocking motion.

This burrowing mechanism is efficient in soft mud, which is viscous and cohesive, and difficult to excavate.

Function of spines related to test shape. The test profile and the morphology of spines in the wedge-shaped type are well designed for the burrowing mechanism of rocking the anterior up and down.

1. *Plastron spines.* The straight and long plastron spines leaning forward, and arranging nearly parallel to the ventral surface, act to push the test obliquely upwards into the frontal sediment (Text-figs 5–6). When the spines are pulled towards the mid-posterior, their tips push down against the floor, and the anterior of the test is raised and pushed obliquely upwards into the frontal sediment. The plastron is wide, occupying one-third of the ventral surface (Text-fig. 6), providing ample space for the spines.

In the wedge-shaped urchins, the plastron spines are necessary for diving into the sediment, which is achieved by a repeated rocking motion created by the thrust of the plastron spines (Text-fig. 9). When the plastron spines were artificially cut off, the urchin could not dive, and merely ploughed around the surface of the sediment, inclined to the surface and with about one-third of the test exposed.

2. *Latero-ventral spines.* The plastron of this type is almost flat, so that only a very narrow space is left between the latero-ventral region of the test and the bottom of the burrow. The latero-ventral spines are smaller and more slender, and attach to the tubercles with smaller areoles than those of other types (Text-fig. 6). The density of the latero-ventral spines of the wedge-shaped *Brisaster latifrons* is about one per square millimetre, which is about a quarter that of the globular *Echinocadum cordatum*. Since the wedge-shaped urchins burrow by pushing rather than by excavating, it is not surprising that the latero-ventral spines which transport the excavated sediment are less developed than those of the other types.

3. *Dorsal spines.* The downward inclining and upward pushing dorsal spines (Text-fig. 6) play an important rôle when they try to return the test to the horizontal. The posture of the spines is more effective at producing an upward stroke to push against the wall and ceiling than the posteriorly inclining dorsal spines. Also, the downward inclination of the dorsal spines interferes less with the oblique upward thrust for forward locomotion.

4. *Anterior spines.* There are no specific excavatory spines on the anterior face of the test. The anterior spines are morphologically the same as the dorsal spines, and push up against the ceiling of the burrow, similar to the dorsal spines.

Function of the wedge-shaped profile. The wedge-shaped profile is essential for forward motion that involves repeated rocking motion rather than excavation. McNamara and Philip (1980) noted that in the schizasterid lineage, the test becomes more wedge-shaped as the sediment grain size decreases. The wedge-shaped profile is generally thought to make burrowing easier in finer-grained sediment (e.g. Smith 1984), because of its streamlined outline. McKinny (1988) suggested that the wedge-shaped profile is effective for excavating the frontal wall of the burrow, because the wedge shape increases the frontal area in contact with the sediment (i.e. increases the scraping spines), without increasing the anterior cross-section (i.e. the sediment to be moved). However, the wedge-shaped schizasterids *Brisaster latifrons* and *Schizaster lacunosus* do not have spines for excavation on the antero-dorsal area, and there are wide frontal ambulacra and anterior petals without spines (Text-fig. 3). It is noteworthy that the burrowing mechanism, which involves pushing rather than excavating in relation to the wedge-shaped test, provides the urchins with a wide antero-dorsal area for the frontal ambulacrum-bearing, funnel-building tube feet and for the respiratory tube feet of the anterior petals.

Burrowing mechanisms of intermediate forms

The functional design of the test and resultant burrowing mechanism of the intermediate urchins can be deduced from the functional morphology of the three extreme types discussed above.

Intermediate between the globular and the flat types. In this intermediate series, two forms of test (low profile and inflated profile) are recognized. In both, the test is lower than the typical globular type, but the shape of the ventral side is similar to that of the globular type, with the elevated plastron and the stern-shaped postero-ventral region (Text-fig. 4). The spines are also the same as in the typical globular form. Accordingly, the basic mechanism of burrowing in the intermediate forms is assumed to be the same as that of the globular type. This was confirmed for *Brissus agassizii*, an inflated form of the intermediate series, in an aquarium with its native sediment.

In these intermediate urchins, low test profile is unlikely to be related to burrowing mechanism. The intermediate test profile is probably an adaptation linked to their burrowing depth, which will be discussed later.

Intermediates between the globular and the wedge-shaped types. The test profiles of *Brissopsis luzonica* and *Hemiaster expergitus* deviate slightly from the typical wedge-shaped test profile, i.e. the overall profile is more globular and tapers less towards the anterior (Text-fig. 4). The plastron region is weakly elevated, and the postero-ventral region is slightly stern-shaped. On the other hand, the morphology of the spines is basically the same as in the wedge-shaped type.

The burrowing behaviour of *B. luzonica* was observed in an aquarium with its native mud. The urchin burrowed to the level where the apex was about 30 mm below the surface. *B. luzonica* burrowed in the same way as the wedge-shaped *B. latifrons*; it dived into and burrowed through the sediment by means of a repeated rocking motion which was less obvious than that of *B. latifrons*.

The intermediate test shape itself may be less optimized for burrowing by means of a repeated rocking motion, although the spines are well designed for it. The urchin lives in muddy sand, a sediment intermediate between those inhabited by the globular and the wedge-shaped types.

OTHER FUNCTIONS OF THE OVERALL TEST SHAPE

Characteristics of test shape that are difficult to explain in relation to the burrowing mechanism are discussed here.

Globular profile of the test

Test profiles of the globular-type urchins are conspicuously high and almost spherical compared with the other types. The shape is apparently inconvenient for burrowing, because it increases the cross-sectional area, and thus increases the sediment volume to excavate.

This shape has probably more significance in maintenance of the burrow wall to prevent suffocation, which is another fundamental problem for infaunal echinoids. Globular-type urchins burrow deeper than urchins of other types. Accordingly, the pressure from the weight of surrounding sediment must be much greater than for other types. A circular cross-section for the tunnel wall is the most effective design for supporting the pressure of the surrounding sediment, and the spherical shape of the spatangoid test may best be explained as an adaptation to support the burrow of the urchin. Thus, the test is comparable to the shield wall of an artificial tunnel, though experimental evidence should be sought for confirmation. The actual shape of such urchins deviates from a sphere, particularly postero-ventrally. The deviation is necessary to enable the urchins to transport and accumulate sediment for locomotion.

According to D. Nichols (pers. comm. 1990), the globular *Echinocardium cordatum* living in sandy sediment around the British Isles have more inflated and globular test profiles than those in mud. This suggests that burrow maintenance is more important in the former. On the other hand, as mud is difficult to excavate, low test profile is probably advantageous when burrowing because of the decrease in the cross-sectional area of the test.

De Ridder (1982) observed that *E. cordatum* feeds only when stationary, and exclusively on surface particles of sediment through the respiratory funnel. Maintenance of the burrow is, therefore, important during feeding in the globular type urchin.

The tests of intermediate forms, such as *Brissus agassizii*, also have a circular cross-section, while the longitudinal section of the urchins is elongate, similar to the flat type, which facilitates burrowing. The intermediate characters are probably related to the shallower depth of burrowing and their feeding on excavated sediments. *Brissus brissus* (Clark 1921), *Meoma ventricosa* (Kier and Grant 1965) and *Brissus agassizii* (my observation) usually burrow 30–50 mm deep, and *Brissus latecarinatus* (Takahashi 1938) 75–100 mm deep. Sediment pressure is less near the sediment surface, and the test is able to adopt a shape more favourable for burrowing. The intermediate urchins have no spines and tube feet to construct a respiratory funnel to the sediment surface. They feed only on the excavated sediment in front of the animal, so that burrowing is only a means to obtain food.

As the intermediate urchins live near the sediment surface, their inflated profiles are apparently unstable and disadvantageous when they are washed out and exposed in currents. The intermediate urchins must burrow deeper in an emergency. They are actually capable of burrowing much deeper than usual: to 100 mm for *M. ventricosa* (Chesher 1969), to 150 mm for *B. brissus* (Clark 1921) and 200 mm for *B. latecarinatus* (Takahashi 1938) and *B. agassizii* (my observation). Chesher (1969) observed that wave action and the resultant disturbance of the surficial sediment caused *M. ventricosa* to burrow deeper. The design of the test, with a circular cross-section, inflated plastron and a stern-like postero-ventral region, must be favourable when the urchins burrow deeply.

Flatness of the test

Tests with flat profiles are frequently encountered in other irregular echinoid groups, such as clypeasteroids. The tendency to be flat first appeared in the Jurassic when the earliest irregular echinoid evolved from a regular echinoid (Kier 1974, 1982). Smith (1984) suggested that the low profile was primarily an adaptation for living on loose, unconsolidated sediment, because the shape would have provided greater stability in currents and brought a larger proportion of spines in contact with the sea floor for more efficient locomotion. Seilacher (1979) noted that the general flattening of the test in clypeasteroids reflects their adaptation to burrowing and feeding close to the sediment surface.

These functional interpretations may be also applicable to the low test profiles of spatangoids, which invariably burrow near the sediment surface. It is noteworthy that urchins with low profiles generally possess spines, which are useful when they are on the sediment surface; long and stout dorsal spines for defence and for righting if the animal is overturned, and large latero-ventral spines (of the flat type) for fast diving. No such dorsal and latero-ventral spines evolved in the globular urchins that burrow deeply.

In the flat type urchin, the flat ventral surface provides space for the latero-ventral spines to give an effective stroke for forward locomotion. The surface, on the other hand, precludes an effective burrowing sole, provides no space for transporting and accumulating excavated sediment, and allows no functional differentiation of plastron and latero-ventral spines. Nevertheless, the urchin still has these spines, although the plastron spines have probably lost significant function. This may suggest that the flat type urchin was derived from urchins with a globular profile, and that the flat ventral surface of the former may be a secondary modification for living near the sediment surface in unstable environments. The fossil record shows that flat type urchins appeared in the Eocene, later than the urchins with globular profiles and inflated plastrons (Fischer 1966).

Domed profile of the test

The test of *Linopneustes murrayi* has a domed profile with a highly inflated dorsal side and a flat ventral side. It is markedly different from the profile of other spatangoids; the flat ventral surface tends to accompany a low test profile. This deviation is easily understandable, because *L. murrayi* lives on the sea-floor in the deep-sea environment. The flat ventral side provides an effective

locomotory sole, while the domed dorsal shape provides a wide area for respiratory tube feet, with loss of petaloid structure. These features are similar to those of epibenthic regular echinoids, and the test shape is more radially symmetrical than in any other spatangoid. These suggest that with release from the functional constraints induced by an infaunal mode of life, the test has returned to an ancestral highly inflated domed shape.

SUMMARY AND CONCLUSIONS

Field observations show that various types of test shape seen in spatangoids correspond to distinctive habitats. In sand-dwelling spatangoids, the test shape is closely linked to burrowing depth.

Spatangoids with flat profiles live near the sediment surface. The flat profile keeps the test stable against current disturbance. In a situation deep below the surface, the globular profile helps to support the burrow wall under greater pressure of sediment. Thus, urchins which live deeper in the sediment tend to have tests more globular in profile. The inflated plastron and the stern-like shape of the postero-ventral region seen in globular type spatangoids is accompanied by the functional differentiation of ventral spines into locomotive and sediment-transporting types; also, these produce the space below and behind the test to allow transport and accumulation of excavated sediment. In contrast, flat urchins living near the sediment surface possess a flat ventral surface which makes the test stable in currents and provides an effective locomotory sole on the sediment surface. Flat urchins burrow by pushing out excavated sediment posteriorly into the surrounding sediment on both sides of the test.

The test shape of mud-dwelling spatangoids is designed to make burrowing easier in soft but cohesive mud which is difficult to excavate. The wedge-shaped profile is essential for the repeated rocking motion that is involved in burial, pushing directly into the sediment rather than excavating it. The wide and flat plastron provides enough space for spines to push up the body at the first step of the rocking motion.

In contrast to the wide variety of the test shapes, spines are similarly arranged among all spatangoids. This indicates that modification of the spine arrangement is probably much more constrained phylogenetically and ontogenetically than is test shape.

The modifications of test shape must have been the major breakthrough that led the spatangoids to adapt a wide range of habitats. It is interesting that holasteroids, another group having the plastron and latero-ventral spines, also show a wide variety of test shapes.

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